

SOME ASPECTS OF THE MORPHOLOGY OF FOUR SPECIES OF THE NEOGASTROPOD FAMILY MARGINELLIDAE WITH A DISCUSSION ON THE EVOLUTION OF THE TOXOGLOSSAN POISON GLAND

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SUMMARY

The living animal, alimentary canal and reproductive system of *Mesoginella* (*Sinuginella*) *pygmaea* (Sowerby), *Volvarina* (*Haluginella*) *mustelina* (Angas), *Volvarinella* *cairoa* (Brookes) from New Zealand and *Diluculum* sp. from the New Hebrides are described. *V. cairoa* has the duct of the gland of Leiblein opening into the buccal cavity and has no buccal mass or radula, whereas the other species have a well developed buccal mass and the gland of Leiblein discharges into the oesophagus behind the nerve ring. An unusual feature of the oesophagus of *M. pygmaea*, *V. mustelina* and *Diluculum* sp. is a tube, derived largely from the ventral channel of the anterior oesophagus, which by-passes the valve of Leiblein and then opens into the mid-oesophagus just behind the valve. The male genital system has a large prostate gland which is closed except for a small posterior opening, and the female system has no gonopericardial canal and has vesicular seminal receptacles that do not ingest sperm. The albumen and capsule glands are similar to those of other Rachioglossa.

An hypothesis is presented on the possible evolution of the toxoglossan poison gland from the combination of the gland of Leiblein, glandular dorsal folds of the mid-oesophagus and ventral channel of the anterior oesophagus.

INTRODUCTION

The marginellids are, with a few exceptions, small animals and probably for this reason are not a 'popular' group like the large, colourful cowries, cones, olives and volutes. They are, never-the-less, allied to the volutes and olives and their beautifully polished shells and handsome animals are extremely attractive.

Although there have been a number of works dealing with the classification of the marginellids these have been based mainly on shell features. Coan (1965) has discussed the taxonomic history of this group and has listed the Recent and fossil genera attributed to the family. He groups the Marginellidae into three subfamilies, each with distinctive radular characteristics, and includes, for the two major groups, information on the external features of the animal of a few species.

Unfortunately the radula and form of the living animal have been described for only a handful of species and only four species are known anatomically. Bouvier (1887) noted the general features of the nervous system of the "Marginellidae" and later (1888) described the oesophagus of "*Marginella*" *cingulata* Dillwin. Eales (1923) has provided some notes on the animal of the Antarctic species "*Marginella*" *hyalina* Thiele and Graham (1966) described the foregut of "*Marginella*" *marginata* (Linné) and "*M*" *desjardini* Marche-Machad. He also included a brief note on

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the female reproductive system of the latter species. Marcus and Marcus (1968) have recently described the anatomy of "*Marginella*" *fraterculus* E. A. Smith.

The following study outlines the morphology of the living animal, alimentary canal and reproductive organs of four species of the Marginellidæ in an attempt to determine some of the morphological characteristics of this family.

TAXONOMY

Of the four species dealt with in this account, three are from New Zealand and one from the New Hebrides. There is no difficulty in identifying the New Zealand material at the specific level but their generic allocations must be reshuffled in the light of Coan's (1965) review.

The most recent attempts to revise the supraspecific status of the New Zealand species of the Marginellidæ were those of Powell (1932, 1952) in which he realigned the New Zealand species of the genus *Marginella* (which included nearly all of the species in the family) into three existing subgenera. No attempt will be made here to reallocate the New Zealand species apart from those actually dealt with. These may be reclassified in narrower groups than at present because they all show considerable differences in their morphology. This need not imply that further genera are necessary for the New Zealand species, as Laseron (1957) has already supplied these in abundance for the closely related Australian fauna.

Mesoginella (*Sinuginella*) *pygmaea* (Sowerby)

1846. *Marginella pygmaea* Sowerby, *Thes. Conch.*, 1: 386, pl. 75, fig. 78, 79.

1932. *Marginella* (*Gabella*) *pygmaea*. Powell, *Trans. R. Soc. N.Z.*, 62: 205, pl. 34, fig. 18; pl. 35, fig. 20 (radula).

Marginella pygmaea agrees very closely with the type species of *Sinuginella* and can be included in that group where Coan (1965) has also placed it.

Laseron (1957) introduced *Mesoginella* and *Sinuginella* on the same page (p.282) with the former appearing first. These two groups differ only in the possession of weak axial ribs by the former, *Sinuginella* being smooth. Coan (1965) has used *Mesoginella* as a genus which includes three subgenera, while *Sinuginella* is treated as a subgenus of *Volvarina*. Thus all factors are not equal in the determination of priority and it is proposed that *Mesoginella* should continue to be used as a full genus with *Sinuginella* as one of its subgenera.

Volvarina (*Haloginella*) *mustelina* (Angas)

1871. *Halina* (*Volvarina*) *mustelina* Angas, *Proc. Zool. Soc.*, p. 14, pl. 1, fig. 5.

1913. *Marginella* (*Volvarina*) *mustelina*. Suter, *Man. N.Z. Moll.*, p. 460, pl. 20, fig. 13.

1932. *Marginella* (*Volvarina*) *mustelina*. Powell, *Trans. R. Soc. N.Z.*, 62: 209.

V. mustelina is the type species of Laseron's (1957) genus *Haloginella* which has been reduced to a subgenus of *Volvarina* by Coan (1965).

Volvarinella cairoma (Brookes)

1924. *Marginella cairoma* Brookes, *Trans. N.Z. Inst.*, 55: 154, pl. 7, fig. 4-5.

1932. *Marginella* (*Serrata*) *cairoma*. Powell, *Trans. R. Soc. N.Z.*, 62: 211, pl. 33, fig. 6.

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Powell (1952) has already indicated that this species should be included in *Volvarinella* Habe. Coan (1954) shows that *Longinella* Laseron is a synonym.

Diluculum sp.

The accurate specific determination of this minute form from the New Hebrides is impossible because of the present state of the nomenclature for Pacific marginellids. A figure of the shell of this species is given and this, together with the other data, should make its future identification possible.

The form of the head of this species closely resembles that of *Euliginella angasi* (Crosse) (Laseron, 1957) except that in the latter species the mantle can be extended over the shell, whereas it cannot in the New Hebrides species. There are also some shell differences; *E. angasi* has additional columellar folds and lacks the narrow parietal callus seen in the New Hebrides species.

Diluculum inopinatum Barnard (1962) has a similar shell and radula to the New Hebrides species. *Diluculum* was reduced to a synonym of *Volvarina* by Coan (1965), and *Euliginella* (which Coan made a synonym of *Cysticus* Stimpson) is probably closely allied to it. The relationships of these two genera and *Cysticus* are discussed below. For the purposes of this account the New Hebrides species can be tentatively included in *Diluculum*, but a definite allocation will not be possible until the head of *D. inopinatum*, the type species of the genus has been examined.

MATERIALS AND METHODS

Both *V. mustelina* and *M. pygmaea* were collected at Leigh, north of Auckland, *V. cairoma* was obtained from Island Bay, Wellington and *Diluculum* sp. from Port Vila, Efate Island, New Hebrides.

All of the material for sectioning was fixed in Bouin's solution and double embedded by Peter's celloidin-paraffin method. It was cut at 6-8 μ and stained in Mallory's triple stain. Specimens were dissected after fixation in formalin and Bouin's solution, and *M. pygmaea* and *V. mustelina* were also dissected alive.

DISTRIBUTION AND HABITAT

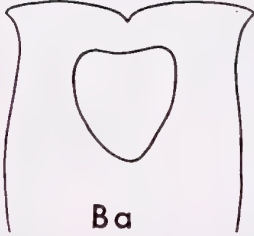
M. pygmaea is found in the North Island where it occurs as far south as Wellington, although it is most abundant on the north eastern coast. This species is generally found from just below low tide level down to several fathoms on coarse, sandy substrate on moderately exposed coasts.

V. mustelina appears to be restricted to the north east of the North Island in New Zealand as it has not been recorded south of East Cape, but it also occurs commonly in the south and south east of Australia, including Tasmania. It is found mainly on semi-exposed coasts beneath stones and in crevices at low tide.

V. cairoma is common throughout the North Island, and it occurs at the Chatham Islands, but there do not appear to be any records of it from the South Island. It is generally found at low tide level living beneath stones, on brown algæ or amongst coralline algal turf.



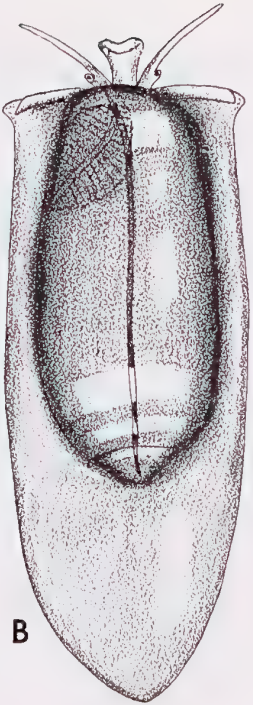
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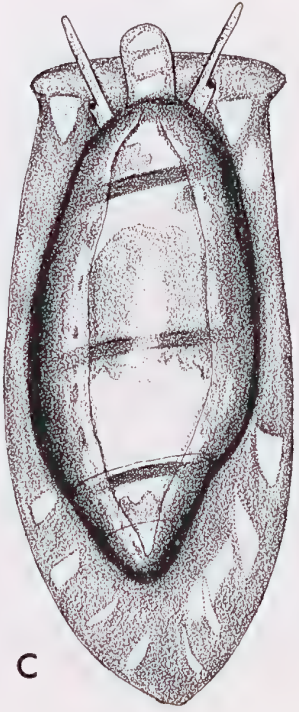
Da



B



A



C

Four living specimens and a few dead shells of *Diluculum* sp. were obtained from Port Vila living amongst short, encrusting brown algæ and corallines in a low tidal pool in sheltered conditions within the harbour.

THE SHELL AND HEAD-FOOT

Mesoginella (*Sinuginella*) *pygmaea*

The glossy, solid shell is generally white or pale yellow and usually varies from 5.5 mm to 6 mm in length and 4.0 mm to 4.8 mm in width. The short spire, thick outer lip, which is smooth within the aperture, and well pronounced anterior and posterior canals, are good recognition features of this species. There are four columellar plaits within the rather large aperture. Powell (1932) has provided a good figure of this species.

The living animal (Fig. 1, A) has a very broad foot which is deeply indented in front and has a large ventral pedal gland in females. There is no operculum. Powerful cilia remove sediment backwards and outwards from the foot, but the delicate mantle edge covering the shell lacks ciliary currents. The foot is opaque yellow and normally has narrow, lateral radiating zones of mixed brown, yellow and orange spots and an anterior triangular area of similar pigmentation. This colour pattern is very variable and sometimes the foot is nearly uniform yellow. The reflected mantle edges covering the shell have black, brown and yellow blotches which are slightly raised as broad pustules. The ground colour is mottled brown, or nearly black, with dense yellow, there being a predominance of the darker colour towards the upper edges. The long tentacles, with the large eyes a little above their outer bases, are translucent with opaque yellow blotches and a few deep orange spots. Small, pale orange spots lie on the opaque yellow, rather long siphon. The superficial pigmentation of the pallial roof can be seen through the dorsal side of the body whorl of the shell and is mottled, greenish-yellow and pale to dark brown or black, the relative density being variable in different individuals.

An allied species *M. (S.) tryphenensis* (Powell), found at Taurikura Bay, Whangarei Heads along with *M. (S.) pygmaea*, has a very similar animal but it has more dark pigmentation and the yellow pustules on the mantle are more distinctly raised.

Volvarina (*Haloginella*) *mustelina*

The handsome, cylindrical shell of this species has a short spire and very long body whorl. The aperture has a distinct anterior and posterior sinus and occasionally the outer lip is covered with denticles, although it is usually smooth. The white shell is ornamented with a broad, median band on the body whorl, with one or two narrow bands above and one on the base. There are four strong plaits on the columella. The shell is usually between 6.2 and 7.0 mm in length and 3.0 and 3.3 mm in width, and has been figured by Suter (1913) and Laseron (1957).

The living animal (Fig. 1, B) has previously been described and figured by Hedley (1916) and Laseron (1957). It is white with a very large foot which is indented in front. There is no operculum, and delicate,

Figure 1. Dorsal view of the living animals of: A — *Mesoginella* (*Sinuginella*) *pygmaea* (Sowerby), B — *Volvarina* (*Haloginella*) *mustelina* (Angas), Ba — Ventral view of anterior end of foot, C — *Volvarinella cairoma* (Brookes), D — *Diluculum* sp., Da — Dorsal view of head and siphon.

smooth mantle edges are reflected over the shell when in the dark. These quickly retract as soon as light falls on the animal. The animal is very active and moves about rapidly, chiefly by ciliary action. Ciliary currents pass around the lower edges of the mantle but the dorsal surface of the foot is unciliated. There is a large ventral pedal gland in females (Fig. 1, Ba). The tentacles are long and slender and the large eyes are a little above their outer bases. The siphon is short.

Volvarinella cairoma

The shell is small, rather thin and semitransparent and elongate oval in shape. It is pale yellowish with a thickened, white outer lip and two narrow brown bands on the body whorl. The rather broad aperture has four columellar folds and there is sometimes a single denticle in the upper third of the outer lip. No anterior notch is developed and the posterior canal is weak. The spire is moderately tall with slightly convex whorls. The shell has been figured by Powell (1932).

In the Island Bay population studied, females were regularly larger than males as shown in the examples below.

Female: 4.4 x 2.0 mm; 4.0 x 1.9 mm; 4.1 x 2.0 mm; 4.1 x 1.8 mm; 4.6 x 2.3 mm.

Male: 3.3 x 1.5 mm; 3.4 x 1.6 mm; 3.6 x 1.5 mm; 3.45 x 1.6 mm; 3.4 x 1.6 mm.

In addition to this difference the colour of the pallial roof, as seen through the shell, is mottled grey in females and black in male specimens.

The living animal (Fig. 1, C) is translucent white with small opaque white patches on the foot, siphon and tentacles. It resembles *V. (H.) mustelina* in the shape of its tentacles and general appearance. The foot has a slightly rounded anterior edge and is tapered behind. Ciliary currents sweep material off the dorsal surface of the foot and others remove particles posteriorly around the mantle edge, which, as in the other species, is capable of being reflected over the shell. A large pedal gland is found beneath the anterior edge of the foot in females.

Diluculum sp.

To facilitate future recognition of this species a figure (Fig. 3, G) and a formal description of it is given.

Shell small, ovate, thin, semitransparent, shining but not glossy, spire very short, $2\frac{1}{4}$ flat whorls. Aperture with a pronounced anterior and posterior canal and 4 columellar plaits, the upper weakest, the lower plait strongest. Outer lip smooth within, inner lip forming a moderately wide, sharply defined callus. A fairly well marked fasciole present. Sculpture of weak growth lines only.

Length 2.3 mm., Diameter 1.5 mm (figured specimen)

Length 2.5 mm., Diameter 1.6 mm (largest specimen)

The shells of this species are housed in the Dominion Museum, Wellington.

The living animal (Fig. 1, D) differs from the three previous species in two respects. The head has the tentacle bases fused ventrally and these

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are extended forward laterally below and beyond the short tentacles (Fig. 1, Da), and in addition, the mantle edges do not appear to extend over the shell. The animal is translucent white with small orange blotches behind the eyes and dense white spots on the head and foot. A few black and orange spots lie on the otherwise white mantle which is visible through the shell. The foot is slightly rounded in front and truncated behind and the short siphon is fused to the head just to the left of the mid-line (Fig. 1, Da).

THE PALLIAL CAVITY

The pallial cavity of the four marginellid species is similar to that of the Olividae (Marcus and Marcus, 1959) and the Volutidae (Ponder, a) and was probably adapted initially in response to a burrowing mode of life. The siphon opens directly above the head, its left margin being fused to the left side of the head. The right corner of the pallial aperture lies far down on the right side, nearly at the base of the cavity. Thus the right pallial wall is considerably shortened and the gonoduct and rectum are consequently displaced and lie nearly transversely across the back of the cavity. A broad, brown, bipectinate osphradium lies alongside a somewhat narrower ctenidium on the left, the latter having broadly triangular filaments. Between the ctenidium and the right edge of the cavity lies a rather narrow hypobranchial gland. This covers the gonoduct and rectum and is pale yellow-brown with scattered dark brown cells in *M. (S.) pygmaea* and *V. (H.) mustelina*. The hypobranchial secretion does not turn purple as in some other neogastropods.

THE RENAL ORGAN AND NERVOUS SYSTEM

The renal organ of all four species has the secondary glandular lamellae separated into an antero-dorsal area whereas the primary lamellae make up the remainder of the renal tissue, with the exception of the nephridial gland. This arrangement is similar to that of the Olividae (Marcus and Marcus, 1959) and the Volutidae (Perrier, 1889) but differs from most other rachiglossan groups.

The nervous system was not studied although it was noted that the circum-oesophageal ganglia are extremely concentrated in the four species examined.

THE ALIMENTARY CANAL

The terminology used for the oesophageal portion of the alimentary canal is that of Graham (1941) and that of the buccal musculature follows Carriker (1943).

Mesoginella (Sinuginella) pygmaea

Only the posterior half of the retracted proboscis (Fig. 2, A; pro) is covered by the rather delicate proboscis sac, the anterior end protruding into an anterior proboscis cavity probably formed by the fusion of the sheath to the body wall. The pleurembolic proboscis is rather broad when retracted, with a blunt distal end and a small, terminal mouth. In section (Fig. 2, B) the proboscis wall is seen to consist of an outer cuboidal, ciliated epithelium, below which is a very delicate layer of circular muscle, but the bulk of the wall, which is only two or three times thicker than the epithelium, is made up of longitudinal fibres. Red

and blue staining gland cells and mucous cells lie in the proboscis hæmocoel around the buccal cavity and the anterior end of the odontophore and oesophagus.

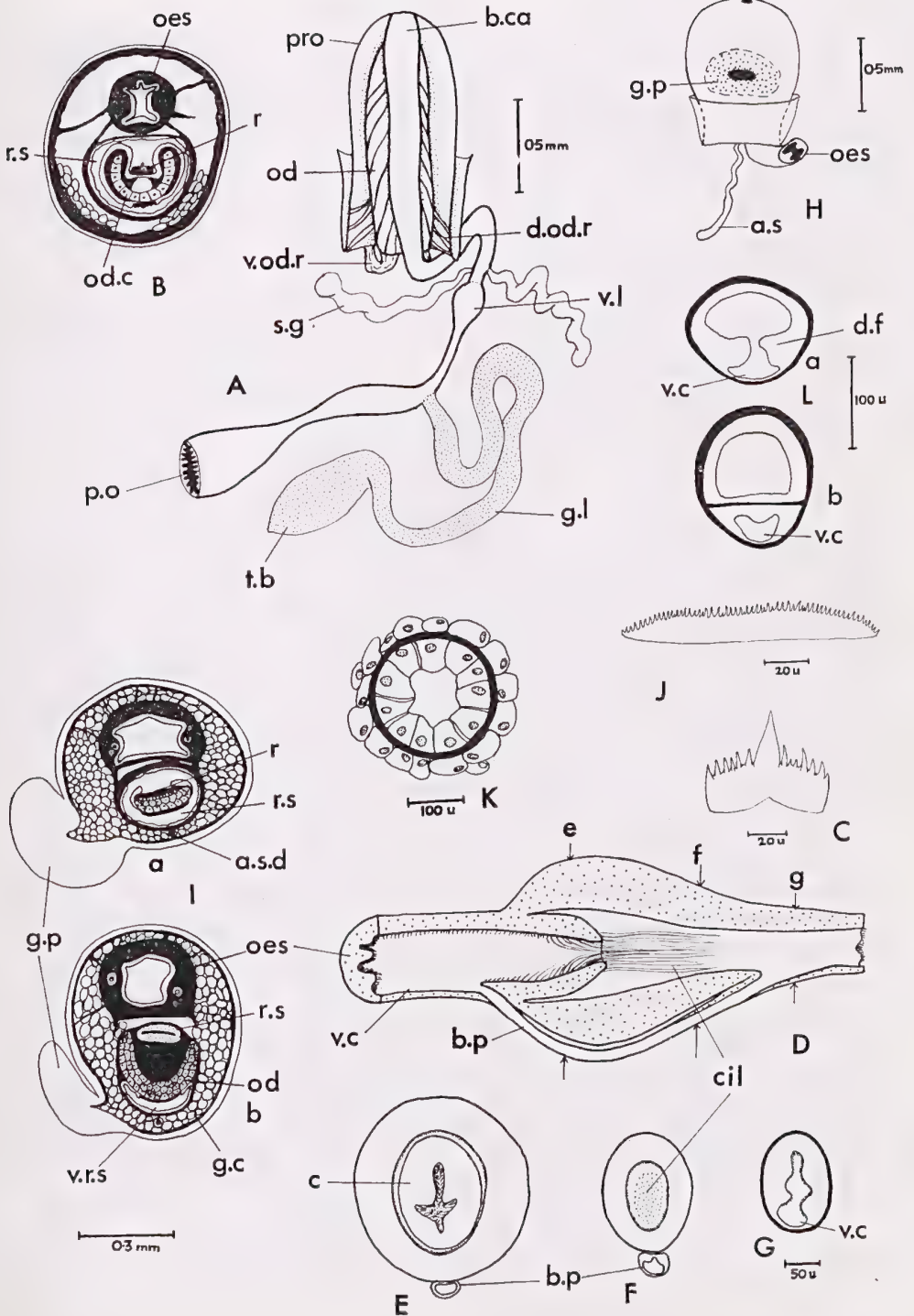
The buccal cavity (Fig. 2, A; b. ca) has muscular walls and a wide, ciliated lumen into which the salivary ducts open laterally just in front of the oesophageal opening, and on the lower side of the dorsal folds. There are no jaws or cuticle lined surfaces and the mouth is only a simple aperture. The œsophagus (Fig. 2, B; oes) has a rather thick wall of circular muscle, is ciliated dorsally and laterally and the epithelium is devoid of gland cells. A few longitudinal muscle fibres can be seen beneath the epithelium and the salivary ducts lie within the well defined dorsal folds. Thin strands of muscle attach the œsophagus to the proboscis wall laterally and dorsally, but the anterior part of the rather massive odontophore (Fig. 2, A; od) is encased below the œsophagus in a common, thin sheath of circular muscle. This structure extends from the buccal cavity to the inner end of the retracted proboscis and has a pair of powerful ventral odontophoral retractor muscles (v.od.r) attached to its posterior end. A few short dorsal odontophoral retractor muscles (d.od.r) are found in the posterior third of the odontophore and are attached directly to the proboscis wall. A conspicuous radular sac (Fig. 2, B; r.s) extends the length of the odontophore, and a series of subradular membrane retractor muscles are attached to it dorsally along its whole length. Thick muscle sheets lying latero-ventrally are the odontophoral protractors and these are continuous with the wall of the buccal cavity in front and are fixed to the posterior end of the odontophore behind. The odontophoral cartilages (od.c) are fused into a single structure in the front half of the odontophore but posteriorly are connected by a transverse muscle in the usual way. The radular sac spreads out in front to encompass the entire anterior end of the odontophore by fusing antero-laterally with its reflected end lying below. Thus the anterior end of the odontophore appears to lie in a separate cæcum as was noted by Graham (1966) in '*Marginella*' *marginata*. The radula (Fig. 2, C) has been described by Powell (1932). It consists of only a single row of

Figure 2. *Mesoginella* (*Sinuginella*) *pygmaea* (Sowerby). A — The anterior alimentary canal showing the proboscis opened dorsally. B — A diagrammatic transverse section through the proboscis near the anterior end of the odontophore. C — Radular tooth. D — A diagrammatic, vertical, longitudinal section through the valve of Leiblein. The arrows indicate the positions of transverse sections E to G. E — A section of the anterior part of the valve of Leiblein. F — A section of the posterior part of the mid-oesophagus just behind the valve of Leiblein.

Volvarina (*Haloginella*) *mustelina* (Angas). H — Ventral view of the proboscis showing the glandular pad. I a-b — Transverse sections through the anterior (a) and middle (b) parts of the proboscis. The glandular pad is displaced to the left in these sections. J — Radular tooth. K — Transverse section of accessory salivary gland. L, a-b — Transverse sections through the narrow part of the mid-oesophagus behind the valve of Leiblein (a is posterior to b).

a.s — accessory salivary gland
a.s.d — accessory salivary gland duct
b.ca — Buccal cavity
b.p — narrow tube below valve of Leiblein
c — cone-like extension of anterior oesophagus forming the valve in the valve of Leiblein
cil — cilia
d.f — dorsal fold
d.od.r — dorsal odontophoral retractor muscle
g.c — gland cells
g.l — gland of Leiblein
g.p — glandular pad
od — odontophore

od.c — odontophoral cartilage
oes — oesophagus
p.o — posterior oesophagus
pro — proboscis
r — radular tooth
r.s — radular sac
s.g — salivary gland
t.b — terminal bulb of gland of Leiblein
v.c — ventral channel
v.l — valve of Leiblein
v.od.r — ventral odontophoral retractor muscle
v.r.s — reflected portion of radular sac.



teeth, each tooth being fairly solid and moderately wide. A long, sharp median cusp is bordered by six or seven short, lateral cusps on each side.

The salivary glands (Fig. 2, A; s.g) are simple tubules and the cells have purplish-red staining granules. They have ciliated ducts which enter the œsophageal wall just in front of the valve of Leiblein. There is no accessory salivary gland.

The anterior œsophagus does not change in structure until just behind the valve of Leiblein (v.l) where the ventral, non-ciliated groove detaches itself and becomes a separate, thin-walled tube (Fig. 2, D-F; b.p) which lies below the valve of Leiblein.

The valve of Leiblein is about twice the diameter of the anterior œsophagus. It has a very thin outer coat of muscle and is lined with relatively tall, blue staining gland cells which have small, wedge-shaped cells between their distal ends. A cone-shaped extension of the anterior œsophagus protrudes into the anterior half of this glandular structure, its long cilia wafting into the posterior half of the valve. The narrow opening of this cone must form a very efficient valve.

The tube derived from the ventral channel of the anterior œsophagus is lined with a pavement epithelium, except below the valve of Leiblein where the latter is reduced in diameter upon entering the circum-œsophageal nerve ring. Here the cells on the dorsal side of the tube become thicker before it becomes confluent with the ventral channel (v.c) of the mid-œsophagus just behind the valve. The low, non-glandular dorsal folds of the narrow part of the mid-œsophagus which passes through the nerve ring, meet and so cut off the ventral channel to form the thin walled, ventral tube. Just behind the nerve ring the œsophagus expands and receives the duct of the gland of Leiblein (Fig. 2, A; g.l) on its right side. The ventral channel, just before this point, swings from its ventral position to the right where it meets the opening to the gland of Leiblein. Torsion is presumably completed just behind this opening. The wall of the mid-œsophagus has a rather thick layer of inner longitudinal and outer circular muscles.

The long, convolute gland of Leiblein (Fig. 2, A; g.l) is the most conspicuous part of the alimentary canal. It is reddish-brown in life and opens into the right œsophageal wall. Most of the gland consists of a long, narrow tube with a small central lumen lined with tall gland cells. A very thin coat of muscle surrounds this part of the gland which lies coiled up in the anterior body cavity. There are three types of gland cell; red, orange and blue staining, and all have basal nuclei and granular cytoplasm. The blue and red staining cells occur throughout in more or less equal abundance, but the orange staining cells are found mainly in the distal part of the tube. Very small ciliated cells lie between the distal ends of the glandular cells in the tube. The terminal bulb (t.b) is wider than the tubular part of the gland and has a thick, external muscle layer composed of outer circular and inner longitudinal fibres. Numerous partitions divide up the interior of this bulb and it is lined with small, irregular cells that bud off their distal ends. The cells contain greenish-brown granules similar to those found in the anal gland.

The posterior œsophagus (p.o) widens behind the opening of the gland of Leiblein into an almost crop-like expansion, but this does not differ histologically from the mid-œsophagus except that the cells are a

little larger and rather more irregular in height, forming about nine low ridges. There is, over the anterior part, an outer wall of circular muscle which becomes very thin a little further behind. The oesophagus narrows as it passes behind the pallial cavity and over the columellar muscle, but it rapidly expands again as it approaches the stomach. At the narrow portion the epithelium abruptly changes to taller, narrower cells which have short cilia and very dense cytoplasm distally. There are no gland cells, and the epithelium is thrown into tall, irregular ridges which have connective tissue and a few muscle fibres in their axes.

The stomach of this species is very similar to that of *V. mustelina* (Fig. 3, A). It consists of a rather small sac into which open the wide, posterior oesophagus (p.o), the rather narrow intestine and a very wide digestive gland duct. The latter has become so expanded that it resembles a caecum, and a wide slit (d.o) at its inner end opens directly into the gland, in which minute fragments of food material can be seen. The gastric epithelium is of columnar cells which bear very short cilia and are thrown into high folds. A wide groove lined with cuboidal cells lies along the antero-ventral wall and leads from the oesophagus to the intestine.

The digestive gland is situated entirely behind the stomach, and a small right lobe lies on the lower edge of the large left lobe. These both open into the same aperture, and are difficult to distinguish. The digestive cells are very uniform and they surround a rather large, single lumen within each lobe. Dense, orange to yellow staining granules are concentrated in the proximal two thirds or half of each cell, the distal part having minute purple or blue staining granules.

The intestine has no gland cells in its posterior section where it leaves the stomach and becomes surrounded by the renal organ. The short pallial section, however, is well supplied with orange to yellow staining gland cells and opens a little behind the exhalant aperture.

A rather conspicuous black anal gland lies near the posterior end of the pallial cavity. It consists of a single branched tubule which opens into the rectum just behind the anus by way of a short, ciliated duct. The epithelium of this gland is non-ciliated and the cells liberate accumulations of very dark green staining granules from small vacuoles. These granules lie loose in the lumen of the gland together with minute purplish staining granules. The latter type are concentrated in the proximal third of the cells where they form a dense mass along with the larger, green staining granules.

Volvarina (Haloginella) mustelina

The alimentary canal of this species resembles that of *M. (S.) pygmaea* fairly closely and only the differences will be noted. The proboscis (Fig. 2, H) has a rounded, slightly bulbous end and is shorter than that of *M. (S.) pygmaea*. A thick pad (g.p) lies on the ventral surface and this is made up of a rim of very elongate, purple staining gland cells that have finely granular contents, which surround a small, central depression. The remainder of the epithelium is of ciliated, short columnar cells which contain a few blue staining gland cells. The muscular part of the proboscis wall is thinner than the epithelium (Fig. 2, I; a, b) and consists of a delicate outer circular layer and a few longitudinal fibres. A mass of gland cells (g.c) fills the proboscis cavity. These are similar

to the cells seen in *M. (S.) pygmaea* but are much more numerous. The odontophore (od) is not as powerful as that of *M. (S.) pygmaea* and, as in that species, extends to the end of the retracted proboscis. A thicker wall of circular muscle surrounds the anterior œsophagus (oes) and the buccal cavity, the latter being lined with short, ciliated, columnar cells. Numerous, fine strands of muscle attach the œsophagus to the proboscis wall. It is ciliated throughout, including the ventral channel, and its lateral and dorsal walls have a few, small glandular cells.

The odontophoral cartilages are fused together apart from a very short posterior portion where the rather weak odontophoral retractor muscles are attached. The subradular membrane muscles are relatively weak compared with those of *M. (S.) pygmaea*, but the radular sac opens out anteriorly in a similar manner. Each radular tooth (Fig. 2, I, J) is about 120 μ across, is low and relatively very wide. It is armed with a series of short, sharp cusps that are rather irregular and variable in shape and size. Powell (1932) failed to find the rather delicate radula of this species.

A short accessory salivary gland (Fig. 2, H; a.s) extends a little behind the proboscis. Its posterior end is only 60 μ in diameter and is lined with relatively large, irregular cuboidal gland cells (Fig. 2, K) which contain bluish staining, finely granular contents and large orange to red staining nuclei. Similar staining oval cells form a single layer on the outer surface of the thin layer of circular muscle that surrounds the lumen. The duct of the gland (Fig. 2, I; a.s.d) opens ventrally into the buccal cavity.

The paired salivary glands each consist of about three tubules, each about 80 to 100 μ in diameter, which lie just in front of the circum-œsophageal ganglia on either side of the valve of Leiblein. A very thin outer wall of connective tissue and a few muscle fibres surround each of the tubules which, themselves, are composed of the normal type of cell with occasional minute ciliated cells. The salivary ducts are constructed like those of *M. (S.) pygmaea* and behave in the same way.

The mid-œsophagus is very like that of *M. (S.) pygmaea* except that the dorsal folds (Fig. 2, L; d.f) are more conspicuous and consist of red staining gland cells. They fuse together (Fig. 2, L) and the ventral channel becomes a separate tube as in *M. (S.) pygmaea*.

The gland of Leiblein is also like that of *M. (S.) pygmaea* except that the glandular section is considerably longer. The gland cells of this section, which are about 30 μ high, show a distinct pattern, although it varies slightly in detail between individuals. A short proximal portion has red staining cells continuous with those of the dorsal folds in the mid-œsophagus, but blue staining cells soon appear in the ventral epithelium and at about one quarter along the length of the tube they are about equal in number with the red cells. The blue cells take over the epithelium almost completely although a few red cells remain scattered throughout the tube. Occasional orange staining cells appear in a narrow dorsal zone when the blue cells become numerous, a little over halfway through the gland they comprise about half of the epithelium, and about two thirds along the length of the tube they form the bulk of the epithelium, sometimes with the complete exclusion of the blue cells. A thin coat of muscle comprised of outer longitudinal and inner circular fibres surrounds this part of the gland. The terminal bulb is about 180 μ .

in diameter (compared with the tube which is 120-150 μ wide), is short and is subdivided by transverse lamellæ. The change in the epithelium between the two regions is abrupt and the outer muscle coat of the bulb is much thicker than that of the tube. An irregular epithelium like that seen in *M. (S.) pygmaea* covers the walls of the bulb.

The posterior œsophagus, stomach (Fig. 3, A) and intestine are like those of *M. (S.) pygmaea*. The cells of the anal gland have fewer green staining granules, and budding cells are infrequent, the majority of the granules being liberated directly from vacuoles as in *M. (S.) pygmaea*. The bulk of the secretion consists of minute, purple staining granules. A single, branched tubule makes up the gland, but this has a very wide lumen in some individuals.

Volvarinella cairoma

The most striking feature of the buccal mass of this species is the complete absence of an odontophore and radula. The proboscis (Fig. 3, B) differs from those of the preceding species in having a sharply pointed distal end and by being lined with a cuticle-covered epithelium anteriorly, although the cuboidal cells have very short cilia posteriorly. There is a moderately thick layer of circular muscle below the epithelium (Fig. 3, Ca, Cb) and about two layers of longitudinal fibres. Most of the proboscis cavity is filled with loose gland cells similar to those in the preceding species, and there are also irregular, thin muscle strands attached to the centrally placed œsophagus. A rather thick layer of circular muscles surrounds the œsophagus (oes) which is lined internally with very small, weakly ciliated cuboidal cells. There is a ventral ridge but no dorsal folds. Below this ridge lies the duct of the gland of Leiblein (d.g.l) (see discussion). On either side of this duct are the inconspicuous salivary ducts (s.d) and below it lies the very narrow accessory salivary gland duct (a.s.d). Near the anterior end of the proboscis the gland cells are largely occluded by a rather dense mass of transverse and radial muscles. The very short buccal cavity, which is lined with squamous epithelium, has a thinner wall than the œsophagus. It is only one fifth to one quarter of the outside diameter of the proboscis. The minute mouth opens directly into the buccal cavity at the tip of the proboscis and, just behind it, opens the accessory salivary gland duct. The duct of the gland of Leiblein opens ventrally into the posterior end of the buccal cavity (Fig. 3, D) whereas the salivary ducts discharge alongside this opening after emerging from a pair of low, lateral swellings that lie in the posterior part of the buccal cavity. These ducts do not extend into the œsophageal wall.

The posterior part of the proboscis contains the salivary glands (s.g) and the accessory salivary gland (a.s), although both also extend into the cephalic cavity when the proboscis is retracted. A thick muscular wall, the longitudinal and circular elements being equal in thickness, surrounds the œsophagus (Fig. 3, Cb; oes) which is narrower in this region. It is lined with strongly ciliated, short columnar cells and it continues unchanged through the nerve ring. Thus the mid-œsophageal region may be represented by this narrow part of the œsophagus but there is no definite indication of the usual mid-œsophageal features.

The salivary glands (s.g) are like those of the foregoing species and extend beyond the accessory salivary gland (a.s) which, just in front of the salivary gland, suddenly narrows to give off its exceedingly narrow,

winding duct. The accessory salivary gland displaces the duct of the gland of Leiblein (d.g.l) so that it lies in a lateral position. This duct is lined with a non-ciliated, cuboidal epithelium and lies below the very narrow part of the œsophagus that passes through the nerve ring but, on emerging behind it, twists to the right and lies above the œsophagus. Although there are four longitudinal ridges in this section of the œsophagus, none of these correspond to the dorsal folds. Behind the nerve ring the œsophagus broadens but the epithelium remains non-glandular and the cells are cuboidal in shape.

The gland of Leiblein (g.l) widens progressively behind and the outer muscle layer increases in thickness. This is mostly composed of longitudinal fibres but there is also a very thin, inner circular layer. Orange, blue and red staining cells make up the glandular epithelium, the orange type being the most abundant posteriorly whereas only blue and red occur near the nerve ring. The terminal bulb is not as discrete as in the other species and the glandular epithelium has invaded its walls, apart from a small pocket in the most posterior part. Here it is lined with a simple squamous epithelium which does not contain any distinctive cytoplasmic inclusions.

The posterior œsophagus can be distinguished a little behind the nerve ring by its taller epithelium which, like the foregoing species, has dense purplish staining contents in the distal ends of the cells. The posterior part is not greatly expanded, however, and has fairly evenly rounded walls which are lined with rather dense staining cells with central nuclei and very short cilia.

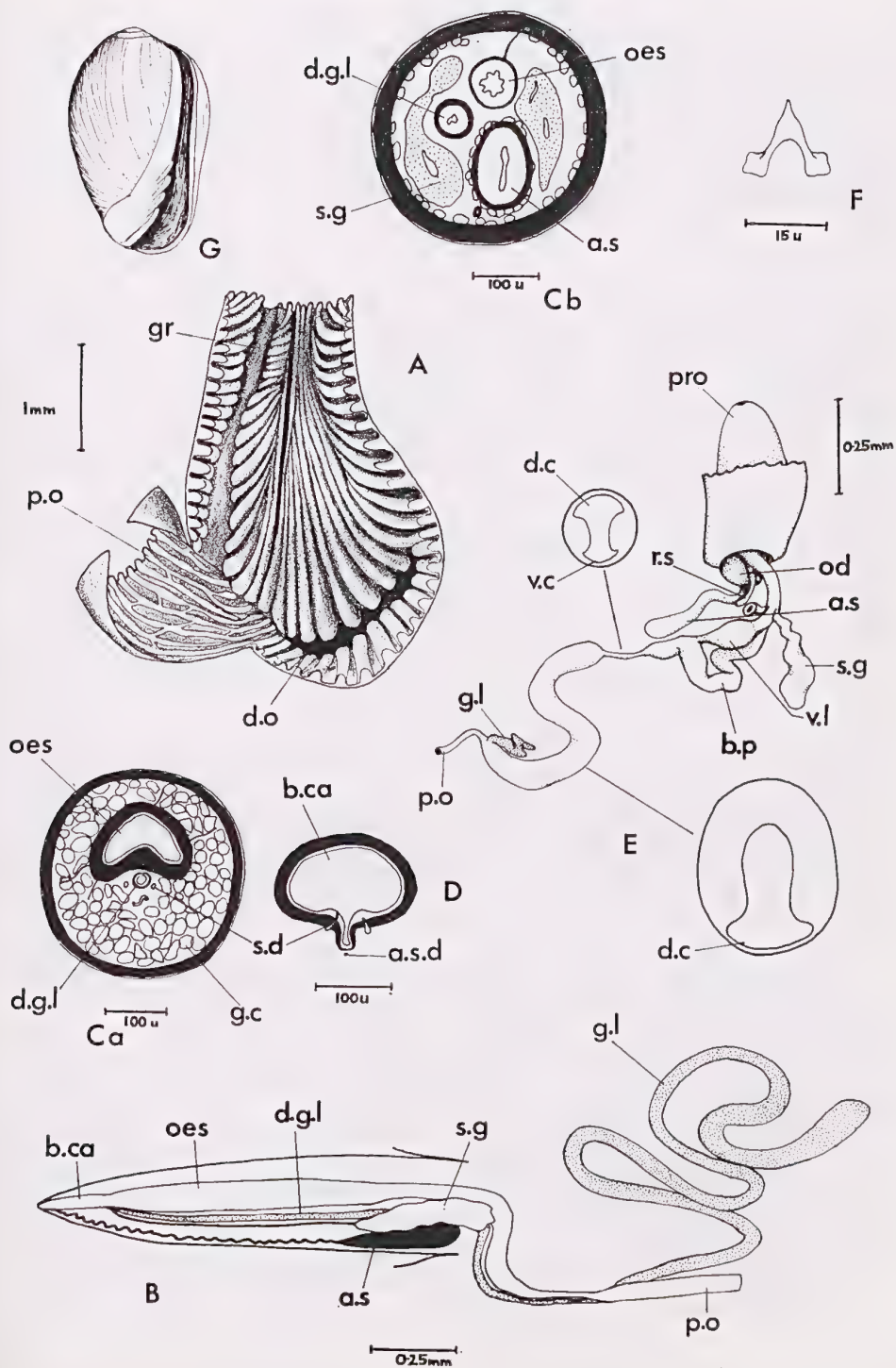
The stomach and digestive gland are like those of the previous species, although the stomach is relatively smaller. As in the previous species the intestine can be divided into an upper non-glandular section which is lined with short columnar cells and a wide pallial portion with a liberal number of orange staining gland cells. This opens into the posterior part of the pallial cavity some distance behind the exhalant opening. The anal gland is a simple, pale brown tube lying along the right pallial wall and it opens well in front of the anus. Posteriorly the cells secrete minute, purplish staining granules, but anteriorly budding is active. There were no large green staining granules in the cells of the anal glands of the specimens sectioned.

Figure 3. *Volvarina (Haloginella) mustelina* (Angas). A — The stomach opened dorsally.

Volvarinella cairoma (Brookes). B — Diagrammatic, lateral view of anterior alimentary canal. Ca, Cb — Diagrammatic transverse sections through the middle (a) and posterior (b) parts of the proboscis. D — A diagrammatic transverse section through the posterior end of the buccal cavity, showing the duct of the gland of Leiblein and the salivary glands opening into it.

Diluculum sp. E — A dorsal view of the anterior alimentary canal showing sections through the mid-œsophagus at the points indicated. The left salivary gland has been removed. F — Radular tooth. G — Shell.

- | | |
|--|---------------------------|
| a.s — accessory salivary gland | od — odontophore |
| a.s.d — accessory salivary gland duct | oes — œsophagus |
| b.ca — buccal cavity | p.o — posterior œsophagus |
| b.p — glandular tube below the valve of Leiblein | pro — proboscis |
| d.c — dorsal channel | r.s — radular sac |
| d.g.l — duct of gland of Leiblein | s.d — salivary duct |
| d.o — opening to digestive gland | s.g — salivary gland |
| g.c — gland cell | v.c — ventral channel |
| g.l — gland of Leiblein | v.l — valve of Leiblein |
| gr — groove | |



It is highly probable that *V. cairoma* is a suctorial feeder and that the transverse muscles surrounding the buccal cavity work in conjunction with the buccal circular muscles and those of the œsophagus, to draw in the food material. Fine particulate remains in the rectum were of variable composition and included algal fragments, diatoms, miscellaneous inorganic particles, and spicules. Possibly this species feeds on the external mucoid secretion of some sedentary animal and could thus pick up a certain amount of debris.

Diluculum sp.

The rather large proboscis (Fig. 3, E; pro) has a blunt end and lies partially within a thin-walled proboscis sac. The small mouth opens into a very muscular buccal cavity which is lined with cuticle ventrally. A very weak layer of muscle surrounding a cuboidal, ciliated epithelium makes up the thin proboscis wall. There are abundant subepithelial gland cells in the anterior part of the proboscis hæmocoel but only a few posteriorly. The œsophagus is narrower and has a thinner wall than that of *M. (S.) pygmaea* and *V. (H.) mustelina*. The relatively massive odontophore (od) has the cartilages separated throughout its length. Thick muscles are attached to the cartilages in the posterior half of the odontophore, but there is only a small amount in the anterior half. A cæcum formed by the expansion of the radular sac (r.s) surrounds the anterior end of the odontophore in the same manner as in *M. (S.) pygmaea* and *V. (H.) mustelina* but the remainder of the radular sac is relatively narrow and extends behind the odontophore. The radula consists of only one row of teeth (Fig. 3, F), these being wish-bone shaped, minute ($15\ \mu$ wide) and very numerous. Each tooth has a short, triangular median cusp and is supported by two, thin, latero-basal projections which have large, club-like ends.

The salivary ducts open in the same way as in *M. (S.) pygmaea* and the glands (s.g), which lie on either side of the œsophagus in the region of the valve of Leiblein, consist of wide, single tubules, their structure being like those of the other species. A rather long accessory salivary gland (a.s) lies behind the proboscis and its exceedingly fine duct opens ventrally into the buccal cavity. The gland is composed of a muscular tube lined with cuboidal cells containing granulate, weakly staining cytoplasm.

The valve of Leiblein (v.l) lies a little in front of the nerve ring and is a simple swelling lined with short, blue staining gland cells. A ciliated cone protrudes into the valve as in the other species. Behind the valve there is a short portion of the mid-œsophagus which has thick, glandular walls and a thin-walled dorsal food groove (d.c). These glandular walls are nipped off just before the valve and continue as a somewhat coiled, glandular tube (b.p) below the valve. This tube opens into the anterior œsophagus in front of the valve after losing its glandular tissue. The gland cells in this tube are identical with those in the mid-œsophagus behind the valve and consist of blue and red staining cells. There are no cilia apart from those borne by a narrow strip of columnar cells which borders the dorsal food groove on either side. The œsophagus narrows as it passes through the nerve ring and is ciliated by the same tracts as in front and behind. A ventral channel (v.c) becomes apparent in this narrow, slightly glandular part, but just behind the nerve ring the œsophagus again expands and at this point the ventral channel swings to the

right and quickly becomes occluded by the glandular tissue. The dorsal food groove (d.c) lies ventrally behind this point, so that in section the mid-oesophagus in front and behind the nerve ring is identical, apart from being reversed.

The posterior part of the mid-oesophagus is long and folded back on itself, and a small narrow, slightly folded gland of Leiblein (g.l) lies at its posterior end. This has muscular walls consisting of inner circular and outer longitudinal fibres and is lined with relatively large cells containing green staining granules. It opens into the oesophagus laterally due to a slight, secondary rotation.

The posterior oesophagus is very like that of *M. (S.) pygmaea* and *V. (H.) mustelina* but does not expand behind the pallial floor. Some of the irregular ridges of the crop are very tall and subdivide the lumen. The stomach is of the same plan as that of *M. (S.) pygmaea* but the gastric lumen appears to be even smaller, the oesophagus and intestine opening very close together. The digestive gland has the normal digestive cells seen in the other species, but in addition has large storage cells with bulging bases and narrow distal ends.

There is a short upper intestine lined with strongly ciliated cuboidal cells with central nuclei, and orange staining gland cells appear at the edge of the pallial cavity. The rectum is very short, the anus lying about halfway along the glandular, pallial gonoduct. There is no anal gland.

THE GENITAL SYSTEMS

The Male Genital System

The male genital system of all the species examined is similar, that of *V. (H.) mustelina* being shown in Figure 4, A. The large testis does not ramify into the digestive gland and it opens into a much coiled vas deferens. This is swollen with stored sperm and thus acts as a seminal vesicle (s.v), but narrows a little way behind the pallial cavity. Here the duct becomes ciliated, the squamous epithelium of the seminal vesicle having changed to cuboidal cells. A short branch from the renal organ (r.o) makes contact with the renal vas deferens but does not open into it. There is no gonopericardial duct, but the vas deferens passes close to the pericardium. Immediately behind the pallial cavity the vas deferens opens into the prostate gland (pr) and at this point a short, ciliated tube in *M. (S.) pygmaea*, *V. cairoma* and *Diluculum* opens into the pallial cavity, but in *V. (H.) mustelina* there is a short slit. The gland itself is rather short and wide in *M. (S.) pygmaea* and *V. (H.) mustelina*, narrower and a little more elongate in *V. cairoma* and folded and doubled back on itself in *Diluculum*. Simple, tall epithelial cells which have red staining secretory granules concentrated especially near their distal ends, surround the narrow lumen, and minute ciliated cells lie between them. There is no trace of a line of fusion showing the position of an originally open groove as in some muricids (Fretter, 1941).

The ejaculatory duct (ej) is rather narrow and is lined with a ciliated cuboidal epithelium, although the proximal region has short, blue staining gland cells. A layer of muscle surrounds this duct, being very thick in *V. cairoma*, moderately so in *V. (H.) mustelina* and thin in the other two species. The duct is unusually long owing to the considerable distance from the exhalant aperture to the base of the penis on the right side of the head.

The structure of the penis shows marked differences in each species so they are described individually below.

The penis of *M. (S.) pygmaea* (Fig. 4, B) is broad, short, flattened and broadly oval in section. Its lateral edges are brown and the remainder white. The circular muscle surrounding the duct is considerably increased in thickness at the base of the penis. The duct lies in the centre of the penis and the remainder of the tissue is made up of loose transverse muscles and fairly dense, blue staining gland cells. A cuboidal epithelium covers the penis, this being ciliated proximally but covered with cuticle distally. The penial duct opens ventrally, just behind the distal edge.

The penis of *V. (H.) mustelina* is about twice as long as that of *M. (S.) pygmaea* and is oval in section (Fig. 4, Aa). Its lateral edges have a rather tall, glandular epithelium which becomes especially prominent near the distal end. The remainder of the epithelium is cuboidal and covered with thin cuticle on the distal part, but is ciliated nearer the base. At the base of the penis the penial duct is narrow, with a ciliated, cuboidal epithelium and a rather thick layer of circular muscle which persists throughout the penis. The duct soon expands and mucous cells appear between the ciliated cells. These are replaced by tall prostatic cells (pr.t) with a few goblet cells lying amongst them. This epithelium persists through most of the penis and this part of the duct takes up much of the bulk of the penis. Numerous subepithelial gland cells, staining orange and purple, lie in the penial tissue around the duct along with scattered muscle fibres. Just behind the distal end the duct narrows and enters a short filament. The outer wall of the penis has only a thin layer of muscle.

V. cairoma has a moderately long penis (Fig. 4, C) which, unlike the preceding species, is divided into two terminal parts; a thick anterior portion which contains the duct, and a posterior, thin-walled sheath (sh) which partially encloses the proximal end of the anterior portion. The thin outer wall has a cuboidal epithelium which is ciliated behind and lined with cuticle in front. Scattered transverse muscles lie in the penial tissue amongst blue staining gland cells. The penial duct resembles the ejaculatory duct in having a very thick wall of circular muscle and a narrow lumen, but it is only about half the diameter. Near the distal end of the penis the duct widens considerably and is lined with blue staining gland cells (Fig. 4, Ca). The ciliated cells are lost and the muscle surrounding the duct is reduced in thickness, whereas the subepithelial gland cells increase in density.

The penis of *Diluculum* sp. (Fig. 4, D) is rather long, slender, and oval in section (Fig. 4, Da) with a very muscular, relatively large, central

Figure 4. A — The male genital system of *Volvarina (Hauginella) mustelina* (Angas). Aa — Transverse section of the penis. B — Penis of *Mesoginella (Sinuginella) pygmaea* (Sowerby). C — Penis of *Volvarinella cairoma* (Brookes). Ca — Transverse section through distal papilla and its sheath. D — Penis of *Diluculum* sp., a — Transverse section. E — Lateral view of the pallial oviduct of *M. (S.) pygmaea*. F, Fa — Dorsal and lateral views of the egg capsule of *V. cairoma*. G, Ga — Dorsal and lateral views of the egg capsule of *V. (H.) mustelina*.

b.c — bursa copulatrix

cap — capsule

ej — ejaculatory duct

i.g — ingesting gland

o.d — renal oviduct

pen — penis

p.o — albumen gland

pr — prostate

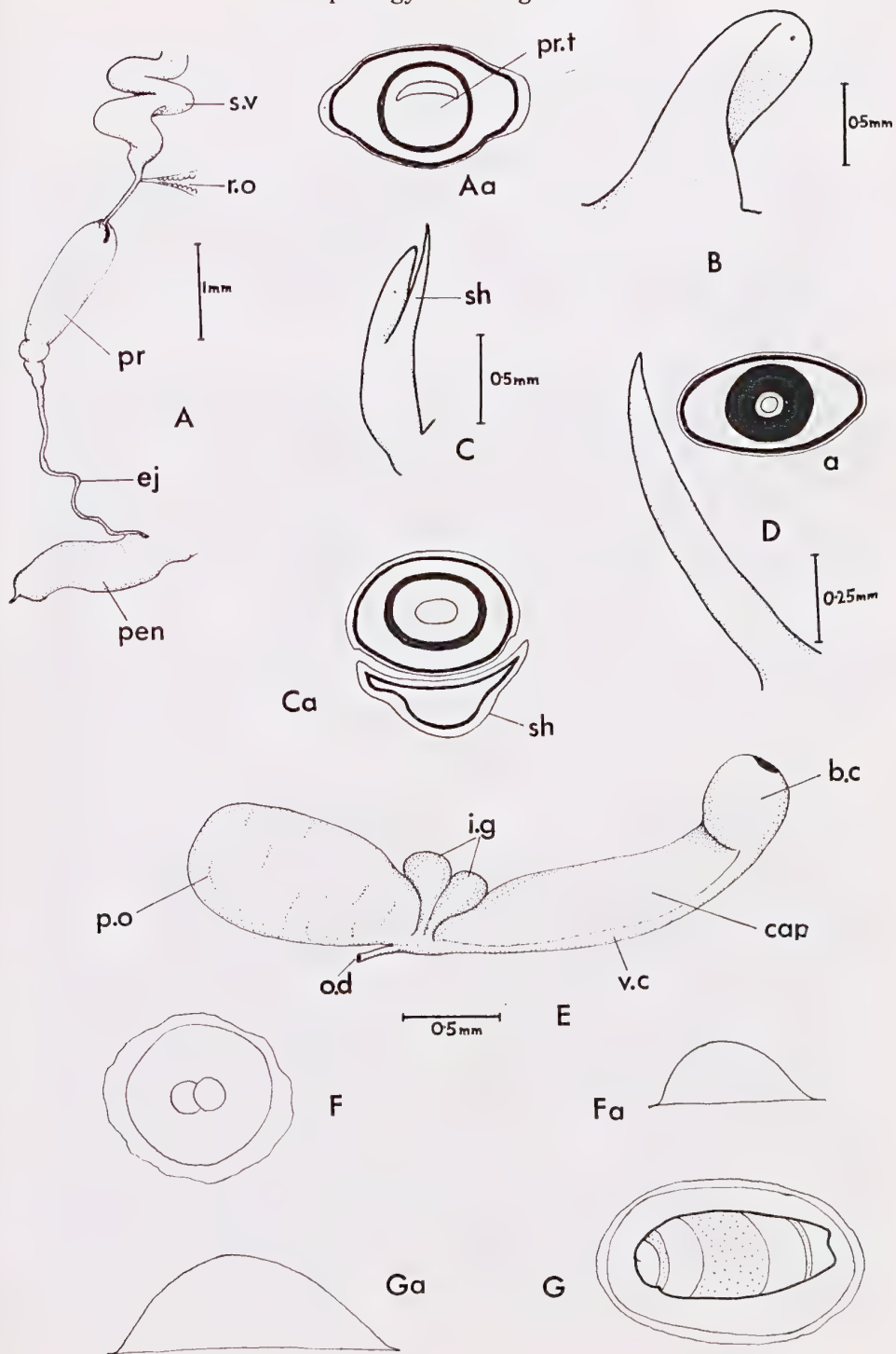
pr. t — prostatic tissue

r.o — branch of renal organ

sh — sheath

s.v — seminal vesicle

v.c — ventral channel of capsule gland



duct. This has a narrow ciliated lumen and the cuboidal lining continues unchanged to the distal end of the penis. The outer epithelium is of cuboidal cells covered with thin cuticle.

The Female Genital System

The female genital tracts of the three New Zealand species are very similar to one another. The pallial oviduct of *M. (S.) pygmaea* is shown in Fig. 4, E. The rather small ovary does not penetrate the digestive gland and contains large yolky eggs. The upper oviduct is a non-ciliated tube, but the wider renal section (o.d) has short, ciliated, columnar cells. There is no gonopericardial canal, but an arm of the renal organ touches, but does not enter, the renal oviduct.

The large albumen gland (p.o) has complexly folded walls and its posterior half lies beside the renal organ behind the pallial cavity. Its glandular walls stain pale reddish and are made up of long, narrow, columnar cells which alternate with wedge-shaped ciliated cells. A short portion of the pallial oviduct between the albumen gland and the capsule gland is a relatively narrow tube with folded, ciliated, non-glandular walls. It receives the renal oviduct below and two or three narrow, ciliated ducts (two in *M. (S.) pygmaea* and *V. (H.) mustelina* and three in *V. cairoma*) which open into an equal number of wide vesicles (i.g) above. These ducts have a cuboidal epithelium and a thin outer layer of muscle. The vesicles, or seminal receptacles, have an irregular lining of cells that are mostly cuboidal in form and variable in size and which have conspicuous, red staining nuclei. The ducts are bound together near their bases by a few common fibres, and at the point where they open into the vesicles there is often a mass of orientated spermatozoa attached to their walls. Groups of sperm can also be seen lying loose in the lumen of the vesicles. No indication of sperm ingestion was observed.

The capsule gland (cap) is a relatively massive structure which, owing to the posteriorly placed exhalant aperture of the pallial cavity, lies transversely across the back of the cavity. The middle glandular region stains orange and there are no clearly marked lateral zones like those seen in certain other rachiglossans. This region has the epithelium arranged in complex units like those in the species described by Fretter (1941) but the glandular regions at either end of the capsule gland have a simple epithelium. In *V. cairoma* there is a zone of mucous cells at both ends of the gland but in *M. (S.) pygmaea* and *V. (H.) mustelina* the anterior region has red staining cells. Some variation in detail was apparent in different individuals of each species. The broad ventral channel of the capsule gland has no prominent ciliated folds overhanging it as in some larger rachiglossans (Fretter, 1941), although there is a rudimentary fold in *M. (S.) pygmaea*. This channel is continuous with the median ciliated region. The short vestibule lies immediately in front of the capsule gland. It has several sharp ridges formed from ciliated columnar cells on its lateral walls. The vestibule opens into the short, thick walled bursa copulatrix (b.c) which lies just in front of the capsule gland and a little behind the exhalant opening. Its walls consist of muscle fibres embedded in connective tissue, and it is lined with ciliated columnar (*M. (S.) pygmaea*) or cuboidal (the other species) cells. The vestibule narrows to form the vagina, a very short ciliated tube which discharges into the bursa just before the latter opens into the pallial cavity terminally.

Morphology of Marginellidae

A large ventral pedal gland consisting of a mass of subepithelial cells can be found behind the anterior edge of the foot in all four species.

The female genital system of *Diluculum* sp. is like that of the other species except that there is only one vesicle making up the seminal receptacle. The capsule gland has no anterior mucous zone and its walls are lined with only a simple glandular epithelium. The vestibule is relatively more spacious and is lined with cuboidal, ciliated cells. Only a few muscle fibres surround the relatively larger bursa copulatrix which is lined with a ciliated epithelium continuous with that of the vestibule in front where these two sections of the duct open together into the pallial cavity. The bursal lining is taller and stains more densely within the bursal lumen.

The egg capsules of only *V. (H.) mustelina* (Fig. 4, G,a) and *V. cairoma* (Fig. 4, F,a) have been found. *V. (H.) mustelina* lays lens-shaped, thin, semitransparent capsules throughout the summer. They are laid in small groups in crevices near low tide mark. *V. cairoma* likewise lays its capsules in groups under clean stones, where they were found nestling in small cracks and crevices in the surface of the stone. The capsules of this species were found at Island Bay, Wellington, in November. In both species only one embryo usually reaches maturity, although in *V. cairoma* at least, two ova are sometimes placed in a capsule. The embryo fills the capsule before emerging as a crawling juvenile.

The capsule of *V. (H.) mustelina* is elongately oval, about 2.75 mm in length and has a narrow, flat margin. The embryo shell is usually about 2 mm when hatched. *V. cairoma* has a circular capsule 1.2 mm in diameter, and the shell of the newly hatched juvenile is of the same length. An irregular flat margin surrounds the capsule in both species.

DISCUSSION

The family Marginellidae

It is clear that further species will have to be examined before a complete diagnosis of this family can be formulated. The range of form in the alimentary canal is considerable and it is highly probable that further modifications will be found. The species investigated by Graham (1966) and Marcus & Marcus (1968) show a different morphology from the species considered in this study and also from one another. This family thus appears to be unlike most rachiglossan groups each of which generally show a remarkable uniformity in the structure of the alimentary canal, but which have considerable variation in shell morphology. In the Marginellidae the difficulty of grouping species into generic units because of the overall similarity of their shells has often been expressed, with the result that the majority of species in most molluscan checklists continue to be retained within one genus, *Marginella*.

Some of the distinctive features of the family shown in the species so far examined, can be summarised as follows: The shell is small to medium in size, usually smooth and glossy, with a thickened outer lip, large body whorl and long, narrow aperture. There are always columellar folds within the aperture and frequently additional accessory denticles. The protoconch is paucispiral and development is thus probably always direct.

The foot is wide but not thick, and there is no operculum. The tentacles usually have the eyes near their outer bases. The siphon is above the head and its left margin is fused to the left side or midline of the head, whereas the exhalant opening is situated almost at the posterior end of the pallial cavity on the right side. The mantle edge is often capable of being reflected over the shell.

Although the proboscis is variable in form it is generally rather short. The buccal apparatus is variable, but when a radula is present the radular sac is expanded and encompasses at least the anterior end of the odontophore. The radula has only the central teeth remaining and these are very variable in form. A single accessory salivary gland is often present and the gland of Leiblein opens either into the œsophagus behind or in front of the nerve ring, or into the buccal cavity. In the case where it opens behind the nerve ring, there is a narrow tube derived from the ventral side of the œsophagus which by-passes the valve of Leiblein. The position of torsion lies immediately behind the nerve ring. The stomach is small, without any cuticle-lined surfaces and usually has a single, wide opening to the digestive gland. An anal gland is usually present. The renal organ has the primary and secondary glandular lamellæ in separate areas and the circum-œsophageal ganglia are highly concentrated. There is no gonopericardial duct in the male or female genital systems and the male has the pallial prostate gland and penial duct closed. The female pallial oviduct has an albumen and capsule gland and usually a small bursa copulatrix. There are one or a few small sperm sacs lined with irregular cuboidal cells. A ventral pedal gland is found in females and the egg capsules are usually lens-shaped and horny.

The accessory salivary gland reaches its greatest development in *V. cairoma* and is also well developed in *V. (H.) mustelina* and *Diluculum* sp. but is absent from *M. (S.) pygmaea* and "*M.*" *marginata*. "*M.*" *desjardini* appears to have an accessory salivary gland which is referred to as a "vestigial buccal pouch" by Graham (1966). No members of the Marginellidæ appear to have paired accessory salivary glands.

Graham has shown that the odontophore of "*M.*" *marginata* lies within a "buccal pouch" derived from the radular sac instead of lying in its normal position on the floor of the buccal cavity. Examination of *M. (S.) pygmaea*, *V. (H.) mustelina* and *Diluculum* sp. show how this pouch is formed. The dorsal and ventral parts of the radular sac become continuous laterally and thus the anterior radular teeth appear to lie naked on the odontophore. The posterior continuation of the expanded anterior portion seen in these three species would provide the situation seen in "*M.*" *marginata* along with the resultant modification of the odontophoral muscles noted by Graham (1966).

The loss of the buccal mass in several species (*V. cairoma*, "*M.*" *hyalina* (Eales, 1923) and "*M.*" *desjardini* (Graham, 1966)), is of special interest as it must necessitate a suctorial method of feeding. There are only a few other stenoglossans that have been reported as having lost the buccal mass entirely, these including certain toxoglossans and the Magilidæ.

The absence of an anal gland in *Diluculum* sp. is probably unusual for the family. The function of this organ is still rather obscure. In *V. (H.) mustelina* the gland often has a very wide lumen in which appears

a finely granular secretion. The anal gland cells in this species, and in *M. (S.) pygmaea*, do not bud off their apices as they do in many stenoglossans. These cells in *M. (S.) pygmaea* contain numerous, dark greenish staining granules which are much more sparse in the cells of *V. (H.) mustelina* and are absent in the anal gland of *V. cairoma*. None of these species have amoebocytes which accumulate dark green granules in their digestive glands, although these are seen in many stenoglossans (Smith, 1967b).

Graham (1966) has described the oviduct of "*M.*" *desjardini* and though he gives no histological details it seems likely that the structure he referred to as a receptaculum seminalis is homologous with the albumen gland of the species dealt with here. The "ingesting gland" of "*M.*" *desjardini* is broken up into several vesicles and is probably equivalent to the seminal receptacles in the species studied here. There is apparently no bursa copulatrix in "*M.*" *desjardini*.

The egg capsules of the two species described here are similar in being domed, oval or circular, thin and transparent, and in having only one embryo develop. The capsules of six species have been described by Knudsen (1950) and except those of "*Marginella*" *cornea* (Lamarck) and "*M.*" *goodalli* which are lens-shaped and have stalked bases, they are similar to those of the New Zealand species. They all contain only one embryo and do not appear to contain nurse eggs, the embryo probably relying only on its own yolk supply.

The real relationships of the relatively primitive *Diluculum* to the remainder of the Marginellidae cannot be satisfactorily established here. The animal of the type species of *Cystiscus*, *C. cystiscus* (Redfield) has been figured by Stimpson (1865) and it has the same anterior expansion of the head seen in *Diluculum* and *Euliginella* (Laseron, 1957), although this appears to have become fused dorsally, whereas in *Diluculum* it remains open. In addition the radula of *C. cystiscus*, also figured by Stimpson, is quite different from that of *Diluculum* sp., although it is strongly arched and this may indicate a relationship. Until the morphology of the alimentary canal of *Cystiscus* is known, *Diluculum* can be tentatively placed within the Cystiscinae.

The Evolution of the poison gland of the Toxoglossa

The derivation of the poison gland of the *Toxoglossa* has never been satisfactorily accounted for and several homologues have been proposed, these including the oesophageal gland (Amaudrut, 1898; Shaw, 1915; Risbec, 1955; Marcus and Marcus, 1960; Kohn, 1963; Graham, 1966), the left salivary duct (Alpers, 1931), and the accessory salivary gland (Graham, 1941; Robinson, 1960 and doubtfully by Marcus & Marcus, 1968). Smith (1967a) suggests that it is an entirely new structure.

Graham (1966) has termed the gland, referred to here as the gland of Leiblein, a poison gland because in one of the species he deals with, "*M.*" *marginata*, the duct of the gland opens into the buccal cavity in much the same manner as does the poison gland of the *Toxoglossa*. This duct opens in a similar position in "*M.*" *fraterculus* (Marcus & Marcus, 1968). In "*M.*" *desjardini*, however, the gland opens ventrally into the oesophagus a little in front of the nerve ring and Graham showed that this gland is orientated in the same way as the oesophageal gland of the Mesogastropoda. Graham followed Amaudrut's (1898) suggestion

that the poison gland was probably stripped off the œsophagus from behind forwards and was therefore derived independently from the gland of Leiblein (see Graham, 1941).

The nature of the "gland of Leiblein" in the Marginellidæ, and in the other rachiglossan and toxoglossan species studied by the writer, suggests the following derivation of this gland in the Marginellidæ, and there is every reason to suppose that the poison gland was derived in a parallel fashion in the Toxoglossa.

The comparatively primitive stenoglossan arrangement of a mid-œsophagus with glandular dorsal folds and a posterior gland of Leiblein is found in several families, including the Muricidæ (Graham, 1941), Olividæ (Marcus & Marcus, 1959), Vexillidæ, Volutomitridæ (Ponder, b), Volutidæ (Woodward, 1900; Pace, 1902) and the Marginellidæ. Amaudrut (1893) and Graham (1941) showed that the gland of Leiblein was formed in most of the Rachiglossa by the mid-œsophageal gland of the mesogastropods being stripped off backwards so that it was connected by a narrow duct opening dorsally into the posterior end of the mid-œsophagus. In doing so a thin-walled groove remained which indicated the line of fusion remaining after the removal of the gland. Although this groove is continuous with the ventral groove in the anterior œsophagus it is thus not homologous with it.

The next stage is apparently the fusion of the apices of the glandular dorsal folds to form a glandular tube with the true gland of Leiblein attached behind by its original duct. This is well illustrated in *Austromitra rubiginosa* (Hutton) and *Vexillum* spp. (Ponder, b), where the tubular part of the gland of Leiblein is in no way differentiated from the glandular dorsal folds lying in what remains of the mid-œsophagus, and a thin walled "scar" is visible along the ventral side of the tube. The original duct of the gland of Leiblein is also visible in species of the genus *Vexillum*. This change appears to be followed by a simplification of that part of the mid-œsophageal region deprived of its glandular tissue, to a simple conducting tube not separable from the posterior œsophagus. Alternatively the atrophication of the mid-œsophagus posterior to the opening of the new duct of the gland of Leiblein and the subsequent forward extension of the posterior œsophagus, would produce the same result.

The stripping off of the dorsal glandular area of the mid-œsophagus must have occurred from behind forwards. The evidence for this in the Marginellidæ is as follows. Firstly, in *Diluculum* sp. similar gland cells to those found in the tube of the "poison gland" of the other species are found in the dorsal glandular area of the mid-œsophagus, and the small gland of Leiblein (sensu stricto) is attached to the posterior end of the mid-œsophagus. Secondly the extension of the stripping off of the dorsal glandular area is halted behind the nerve ring in *M. (S.) pygmaea* and *V. (H.) mustelina*, but in the latter species the glandular tissue of the œsophagus and tube are continuous. In addition a tubular loop representing the lower half of the dorsal folds (this area being pre-torsional) and the ventral channel, by-passes the valve of Leiblein to become confluent with the ventral channel of the anterior œsophagus. The same by-pass is found in *Diluculum* sp. but in that species it is glandular. "*M. desjardini*" (Graham, 1966) indicates the next stage in having the duct of the gland continuous with the tubular by-pass through

the nerve ring, and so past the valve of Leiblein to open into the anterior œsophagus. This step could be achieved by continuing the pinching off of the ventral channel through the nerve ring. *Volvarinella cairoma* shows how further anterior extension of the poison gland probably took place. In this species the narrow duct of the poison gland opens ventrally into the buccal cavity as it does in "*M.*" *marginata* (Graham, 1966) and "*M.*" *fraterculus* (Marcus & Marcus, 1968). The duct lies beneath a median, ventral ridge in the anterior œsophagus which almost certainly represents the fused dorsal edges of the dorsal folds. This is indicated by the occurrence of two separate folds in the most posterior section of the anterior œsophagus which quickly fuse to form the median fold. There are, in addition, two low swellings in the buccal cavity which probably represent the dorsal folds. No other structures occur within the œsophagus that could represent these folds, although they are prominent in the other species. It would appear then, that the apices of the dorsal folds have become fused so that their ventral portions, and the channel between them, have been nipped off and lie as a separate duct. This is merely an anterior extension of the by-pass beneath the valve of Leiblein which opens ventrally into the posterior end of the buccal cavity.

The salivary ducts are typically embedded in the œsophageal wall beneath the dorsal folds, but in *V. cairoma*, "*M.*" *fraterculus*, and in "*M.*" *marginata* they lie free owing to the dissociation of these folds. "*M.*" *desjardini* also has free salivary ducts which apparently run outside the œsophageal wall in front of the point where the "poison gland" becomes confluent with the anterior œsophagus. This, however, may be due to an independent stripping of the salivary ducts from the proboscis wall as has occurred in several groups (e.g. some Buccinidæ (Dakin, 1912) and some Mitridæ (Risbec, 1928)).

The terminal sac of the "poison gland" is, as shown above, equivalent to the gland of Leiblein (*sensu stricto*) of the Muricidæ and Buccinidæ, as it generally has a similar histology, and has the same morphological relations. The glandular activity is, however, usually much reduced. The cells can be characterised by their very irregular shape, the budding of their distal ends and the production of greenish-brown staining granules. It is these granules that give the gland its characteristic brown colour in life. Similar cells have been observed by the writer in the terminal sac of the poison gland of certain Turridæ, notably *Leucerapeus angustatus* (Powell) and *Maoritomella albula* (Hutton). This sac becomes a muscular bulb in the toxoglossa that pumps the secretion formed in the duct from the gland.

The anterior migration of glandular tissue through the duct of the poison gland could readily occur once the duct had been freed from its morphological straight jacket, and thus the whole nature of the anterior and mid-œsophagus could be altered. A duct derived in the above way would follow the same path around the œsophagus as would a derivative from the œsophageal gland.

Most toxoglossans are at a stage comparable with those marginellids with a radula. Some have lost this structure and thus resemble *V. cairoma*. All of the toxoglossans that have been investigated either have a fully developed poison gland or have lost this structure. There are no dorsal folds in the œsophagus and the salivary ducts are always free from the œsophageal wall. The main difference from the Rachiglossa lies in the

very much shorter anterior œsophagus, if indeed this can be distinguished at all.

One notable absence in the alimentary canal of the *Toxoglossa* is the valve of Leiblein (Smith, 1967a). This is also absent in *V. cairoma* and is not mentioned in either of the species studied by Graham (1966) but in "*M. fraterculus* a slight swelling in interpreted as an "individually inconstant valve of Leiblein" by Marcus & Marcus although there was no histological verification. Its efficiency as a valve in the three marginellid species which possess it is undoubted, because of the extreme development of the valvular cone and the lack of a ventral groove through this structure. The necessity for the by-pass tube could possibly be associated with allowing the forward flow of the secretion from the "poison gland", or alternatively, a safety valve useful during the sudden contraction of the proboscis. The former function would allow retention of the valve after the incorporation of the by-pass tube in the poison gland duct, but the latter would not. It is of interest to note that most rachiglossan species not having a gland of Leiblein have also lost the valve of Leiblein.

In summary the "gland of Leiblein" of the Marginellidæ and the poison gland of the *Toxoglossa* were probably formed in the same way. This involved the formation of a long duct to the gland of Leiblein (*sensu stricto*) by the fusion of the apices of the dorsal folds of the œsophagus which passed through the nerve ring and entered the buccal cavity. The glandular tissue of the mid-œsophageal section of the dorsal folds migrated anteriorly. This was accompanied by a reduction in the glandular activity of the gland of Leiblein, this becoming the terminal sac of the marginellid "gland of Leiblein" or the muscular bulb of the toxoglossan poison gland. The by-passing of the valve of Leiblein was accompanied by its reduction and eventual loss.

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